

Future Consequences of Climate Change for the Chesapeake Bay Ecosystem and Its Fisheries

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Abstract.—Chesapeake Bay supports a number of valuable fisheries within its boundaries and serves as an important nursery area and seasonal feeding ground for many coastal Atlantic species, despite substantial anthropogenic modifications to the ecosystem for more than two centuries. Ecosystem managers are now confronting the fact that future climate changes may be superimposed upon continued coastal development, resource exploitation, and regional human population growth. As an estuarine ecosystem, Chesapeake Bay is particularly sensitive to long-term changes in three major hydro-climatic variables: temperature, sea level, and precipitation/riverflow. Based upon historical trends and model projections, relative sea level will likely continue to rise and temperature is more likely to increase than decrease. Future changes in precipitation and riverflow are highly uncertain. As relative sea level continues to rise, erosion of coastal margins will likely increase turbidity and may decrease the extent of submerged and emergent vegetative habitats. This would have far reaching effects because these habitats are important nursery areas for many Chesapeake Bay and coastal Atlantic fish populations. Increased temperature would likely result in increased utilization of Chesapeake Bay by subtropical species such as brown shrimp (*Farfantepenaeus aztecus*) and decreased utilization by cooler water species like striped bass (*Morone saxatilis*). Changes in riverflow would affect nutrient and dissolved oxygen levels, salinity distribution, and estuarine circulation. Also discussed are more complex changes that are dependant upon the rate of change, magnitude, and seasonal timing, of these climate variables. Within the context of precautionary management principles, Chesapeake Bay ecosystem management must consider that future climate changes could alter species composition, distribution, and diversity within the Bay and influence Chesapeake Bay and coastal Atlantic fisheries production.

Introduction

Chesapeake Bay (Figure 1) is one of the largest and most productive estuaries in the world (NOAA 1985, 1990). Annual commercial fisheries landings data (NMFS 2001) reveal that Chesapeake Bay dockside value for the year 2000 totaled more than US\$172 million, accounting for 5% of the harvest value from all states combined. Although these figures are significant, they understate the value of the Chesapeake Bay ecosystem

because they do not account for the ecological services the Bay provides to coastal Atlantic fisheries. Chesapeake Bay is an integral subsystem of the Northeast U.S. Continental Shelf Large Marine Ecosystem (Sherman et al. 1996), serving as an important seasonal feeding ground and nursery area for ecologically and economically important coastal species that range from Florida to the Canadian Maritime Provinces. Examples include Atlantic menhaden *Brevoortia tyrannus*, striped bass *Morone saxatilis*, spot *Leiostomus xanthurus*, summer

flounder *Paralichthys dentatus*, Atlantic croaker *Micropogonias undulatus*, and the alosids, including American shad *Alosa sapidissima*, alewife *A. pseudoharengus*, and blueback herring *A. aestivalis*.

Considering both the economic and ecological importance of Chesapeake Bay, it is important to undertake an initial assessment of the potential consequences of future climate changes for the ecosystem and its fisheries. Unfortunately, it is not currently possible to use results from general circulation models (GCMs) to accurately predict the response of biological systems to regional climate changes induced by the continued addition of radiatively active (or 'greenhouse') gases to the atmosphere. While state-of-the-art GCMs "provide credible simulations of climate" at "subcontinental spatial scales and over temporal scales from seasonal to decadal" (Houghton et al. 2001), this resolution is far below that required to resolve potential changes in many biologically relevant events and processes, which can occur on scales of meters to kilometers and weeks to months. In fact, regional-scale GCM projections for some ecologically important climate variables (e.g., precipitation) differ in timing, magnitude, and even sign (increasing versus decreasing), depending upon which combination of model and emission scenario is used (NAST 2000; Houghton et al. 2001).

With these limitations in mind and because no single climate model can be considered 'best' (Houghton et al. 2001), we consider how projected changes in water temperature, sea level, and streamflow between the years 2000 and 2030 may affect the Chesapeake Bay ecosystem and its fisheries. In this evaluation, we utilize projected changes in these three variables as presented in the U.S. Global Climate Change Program's recent Mid-Atlantic Regional Assessment (Fisher et al. 2000; Najjar et al. 2000). Those projections were based upon climate change simulations from both the Canadian Climate Center (CCC) and United Kingdom Meteorology Office's Hadley Center GCMs. Model simulations were run from the mid-19th through the 21st centuries and driven with actual global emissions until 1990. After 1990, global carbon dioxide emissions were increased by 1% per year. The effects of sulfate aerosols were also included in both models. We also compare these model-derived predictions to current trends in Chesapeake Bay water temperatures, sea level, and streamflow.

Anticipated Changes

GCM Projections and Their Uncertainties

The level of uncertainty in projected changes in temperature, sea level, and precipitation (which influences

streamflow) is related to the level of complexity in the relationship between each variable and the atmospheric concentration of radiatively active gases. First proposed by Svante August Arrhenius more than 100 years ago (Fleming 1998), the relationship between carbon dioxide concentration and atmospheric temperature is direct. Najjar (1999) found that air temperature accounted for between 68% and 93% of the variance in upper Chesapeake Bay water temperature, which is little influenced by Atlantic Ocean temperature. This evidence suggests that, although there is considerable uncertainty in the regional projections of the climate models themselves, the air temperature rise of between 1.0°C and 1.5°C projected in the Mid-Atlantic Assessment should result in a comparable increase in Bay water temperature.

Sea level rise is a second order response. It is dependent not only on changes in atmospheric temperature, but also on changes in the amount of ice stored in glaciers and land-based polar ice caps. Global sea level has been rising and is expected to rise at faster rates (Gornitz et al. 1997), if only because of ocean water thermal expansion (Russell et al. 2000). The added level of complexity in projecting sea level change (as a secondary response to warming) is reflected in the relatively wide range in the Mid-Atlantic Regional Assessment's projection of a rise between 11 cm and 31 cm by 2030 (Fisher et al. 2000; Najjar et al. 2000).

Predicting future changes in regional precipitation patterns is an even more complex problem than projecting future sea level changes. This is because precipitation patterns depend both upon temperature and atmospheric processes that occur on scales much finer than the resolution of current GCMs. For example, while temperatures are reasonably well modeled by coupled GCMs, these models do not accurately represent precipitation events, at least in part because intensities and patterns of precipitation are strongly influenced by local scale features and processes (Houghton et al. 2001). Accurate forecasts of future streamflow is an even more difficult proposition, since streamflow is influenced not only by precipitation magnitude and intensity, but also by other variables that are likely to change with rising temperatures such as evapotranspiration, soil moisture, and land use patterns.

These uncertainties preclude confident and specific projections of the effects of climate change on the Chesapeake Bay ecosystem and its fisheries. However, an early assessment of possible changes is needed because managers need significant lead-time in order to justify, plan, and initiate precautionary or mitigating management strategies designed to protect ecosystem integrity and ensure sustainability for the Bay's fisheries. For this reason, we considered the Hadley and CCC GCM projections of future changes in these variables reported by

the U.S. National Assessment (NAST 2000), as well as historical trends evident in available water temperature, sea level, and streamflow data for Chesapeake Bay.

Current Trends

Increased emissions of carbon dioxide associated with the industrial revolution resulted in a rise in atmospheric concentration that exceeded natural background levels around the mid-19th century (Etheridge et al. 1998). Because excess CO₂ has been accumulating in the atmosphere for more than a century, contemporary trends in ecologically important variables such as water temperature, sea level change, and streamflow may be instructive when assessing the effects of climate change on the Chesapeake Bay ecosystem and its fisheries.

Water temperature in the York River has been measured from the pier of the Virginia Institute of Marine Science (Figure 1) since 1957. Our analysis of annual average temperatures for each calendar month revealed significant positive trends for December, January, and March–August, excluding May (Figure 2). These results are generally consistent with annual warming trends (0.18–0.45°C/decade) reported by NOAA's Climate Prediction Center during the last four decades for southeastern Virginia (<http://www.cpc.ncep.noaa.gov/antrend.gif>).

Increased shoreline erosion and inundation, resulting from sea level rise, are the consequences of global climate change that are most often associated with coastal environments. Indeed, postglacial sea level rise during the Holocene created the Chesapeake Bay and other drowned river valley estuaries (Colman et al. 1992). Regionally observed sea level rise over recent millennia is mainly the result of geological subsidence that has occurred in this coastal region since deglaciation. Although glaciers did not extend as far south as the Chesapeake, they caused a peripheral land surface bulge, uplifting the Bay region. With the weight of glaciers removed, the crust is now subsiding.

Throughout most of the last millennium, sea level has been relatively static, rising at a rate of only 1–2 mm per year in the Chesapeake Bay region (Kearney 1996). However, during the 20th century, tide gauge records indicate that relative mean sea level rose at 3–4 mm per year in the Bay region (Titus and Narayanan 1995). Relative sea level rise rates appear to have been greater, however, in local areas within the Bay where large groundwater withdrawals caused greater subsidence of coastal land and wetlands, such as Blackwater marshes near Cambridge, Maryland (Stevenson et al. 1986; Wray et al. 1995). Furthermore, over some multiyear periods, sea level has risen as much as 10 mm per year at some gauging stations (Stevenson and Kearney 1996). These relatively short-term and rapid

risers in sea level along the Atlantic Coast appear to be the result of very low-frequency waves generated by wind stress over the open ocean (Hong et al. 2000).

Chesapeake Bay flow was also analyzed for trends that may be indicative of future climate changes. The U.S. Geological Survey (USGS) provides estimates of streamflow input to Chesapeake Bay since 1951 using methods developed by Bue (1968). These data are available for five cross-sectional transects within the Bay. Using data for transect E (Figure 1), we analyzed monthly Chesapeake Bay discharge annual time series for February, March, and April. We chose these months because the Hadley and Canadian Climate Centre GCM scenarios used by Fisher et al. (2000) indicated that streamflow would change the most during this period (Figure 3). Streamflow during this late winter–early spring period is ecologically important because it strongly influences the ecosystem by influencing the nature, timing, and magnitude of the annual spring phytoplankton bloom. In contrast to temperature and relative sea level data, no long-term trends were detected in streamflow.

Considering available temperature, sea level, and streamflow data and the latest model-based assessment of climate change in the Chesapeake Bay region (Fisher et al. 2000), we assume with reasonable confidence that the rates of temperature and sea level rise for the Chesapeake Bay region during the last four decades will at least continue, or more likely increase, over the next century. Subsequent sections of our paper address the potential consequences of these changes. Because streamflow data and model projections are less clear, we also consider the effects of increases and decreases in freshwater input to Chesapeake Bay.

Consequences for the Chesapeake Bay Ecosystem and Its Fisheries

Temperature

Persistent long-term rise in mean annual water temperatures will certainly alter the seasonal distribution patterns of ecologically and economically important fishery species of Chesapeake Bay. Future warming will likely result in a shorter (climatological) winter season and allow for earlier spring immigration and later fall emigration of the many coastal species that utilize the Bay as a seasonal feeding ground or nursery area.

As warming progresses, it will differentially affect subtropical and cold-temperate species. Subtropical species will benefit from warmer temperatures and may increase their utilization of the Bay as a feeding ground, spawning ground, and nursery area. Conversely, warming will limit the use of Chesapeake Bay by cold-tem-

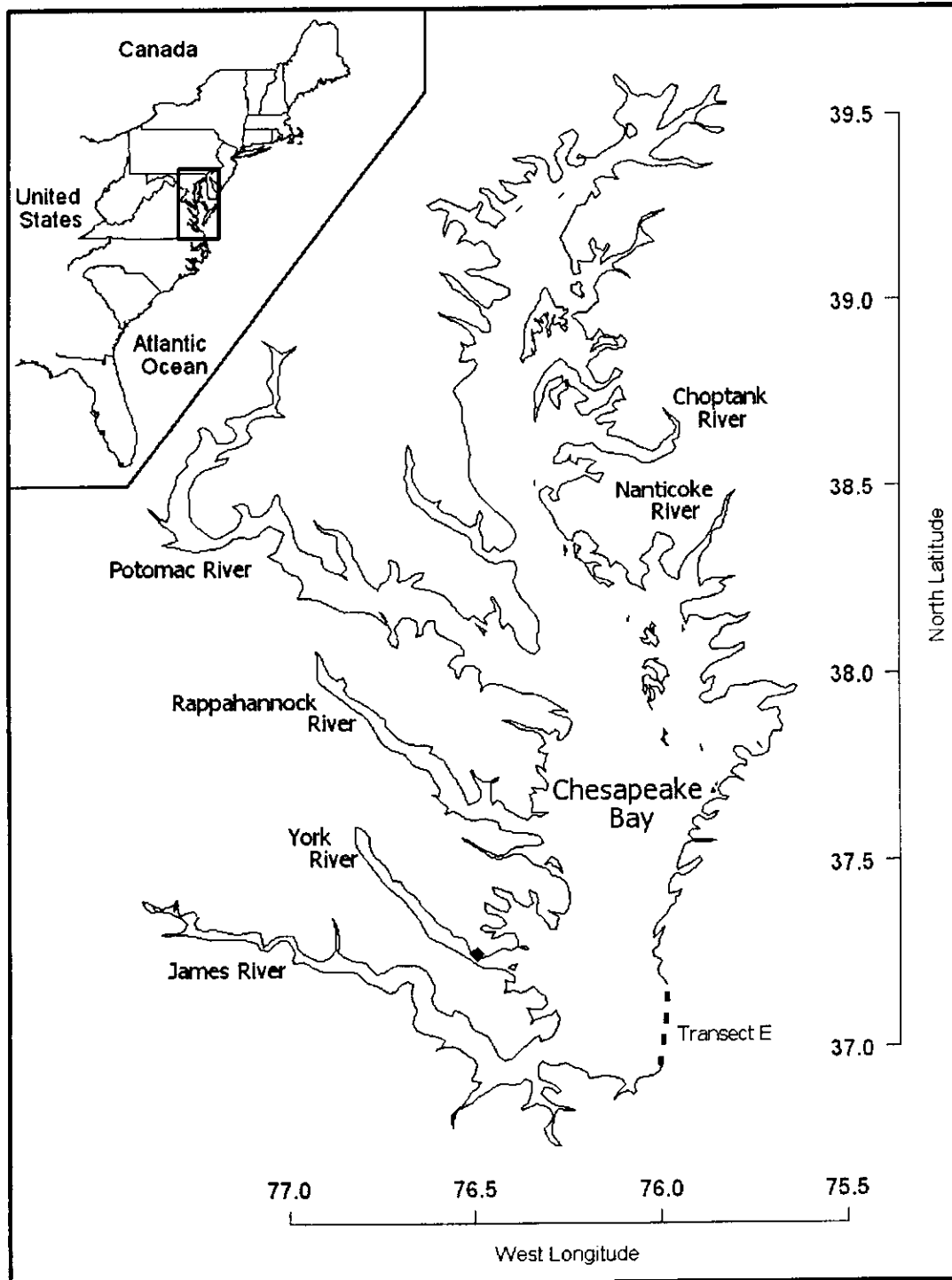


Figure 1. Map of Chesapeake Bay and its major tributaries. Flow of the Susquehanna River, the Bay's largest tributary, enters at the head of Chesapeake Bay (not labeled). Collection site for temperature data presented in Figure 2 (black diamond) and the transect used for Chesapeake Bay flow trend analysis (dashed line) are shown.

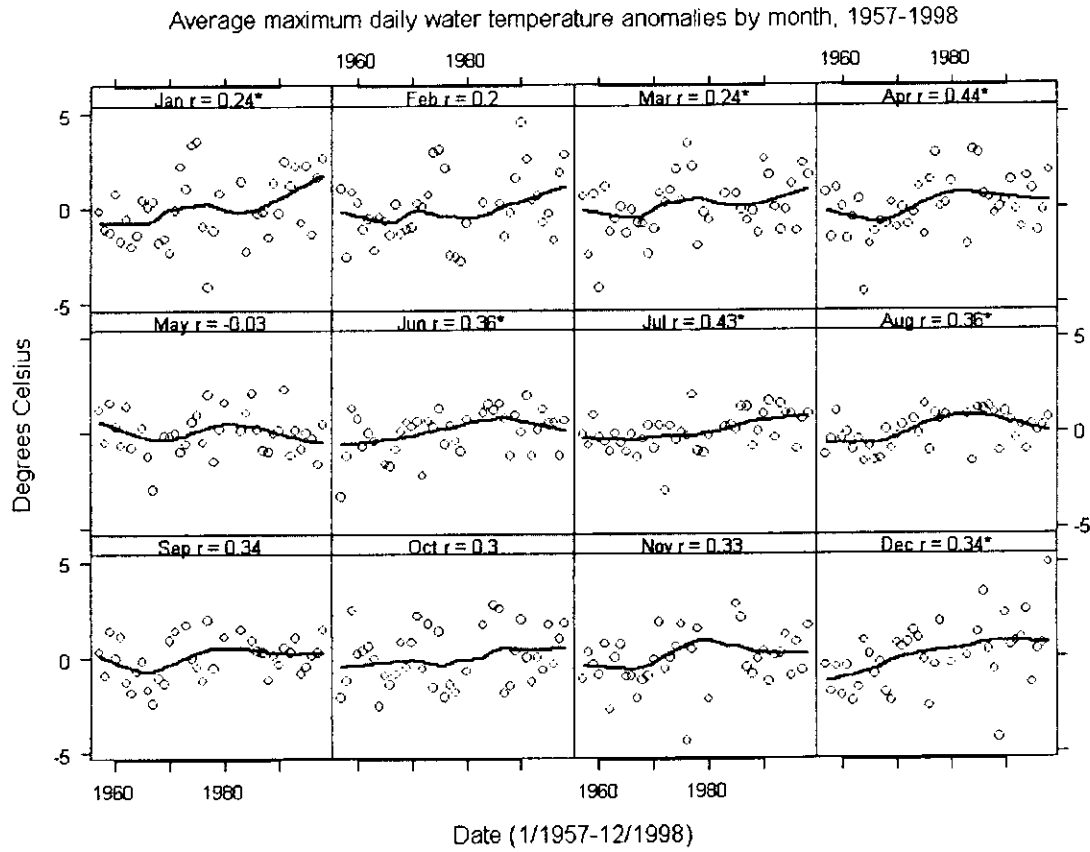


Figure 2. Trend analysis of monthly mean water temperature anomalies (1957–1998). Temperature measurements were collected from the pier of the Virginia Institute of Marine Science at the mouth of the York River in the lower Chesapeake Bay. Daily maximum temperatures were averaged for each month. Anomalies were calculated by subtracting each month's average daily maximum temperature over the study period from its respective monthly time series. Correlation (r) values between temperatures and year are provided. Asterisks indicate significant trends evaluated at the 0.05 level. Lowess smoothing (solid lines, span = 0.5) is used to depict decadal-scale patterns in the time series. Source: VIMS scientific data archive, 2001 (<http://www.vims.edu/resources/databases.html#pier>).

perate species. Warmer temperatures will decrease the areal extent of bioenergetically favorable Bay habitats for these species during the growing season because warmer temperatures increase metabolic costs and decrease dissolved oxygen content (Coutant 1985; Coutant and Benson 1990).

Warming water temperatures are most likely to affect Chesapeake Bay species possessing northerly ranges that end in the Mid-Atlantic. For example, the commercially important soft clam *Mya arenaria* is near its southern distribution limit in Chesapeake Bay and may be extirpated if temperatures approach and remain near 32°C (Kennedy and Mihursky 1971). A positive effect of warming in the mid-Atlantic region, where severe winters are thought to result in low blue crab catches (e.g., Pearson 1948), is that less severe winters may en-

hance harvests. Warmer conditions might also allow populations of some subtropical species, such as shrimps of the genus *Farfantepenaeus*, to increase and support viable fisheries in the Chesapeake Bay and the Mid-Atlantic Bight.

While it is likely that a prolonged warming will lead to a shift in the ecosystem favoring subtropical species over temperate species, physical or ecological factors other than temperature may preclude a smooth transition to a balanced ecosystem dominated by subtropical fishery species. For example, many Bay species depend on coastal and estuarine circulation patterns to distribute their planktonic egg and larval stages into suitable nursery areas (e.g., Epifanio and Garvine 2001). It is difficult to predict how coastal or Bay circulation patterns may change in the future because they will be si-

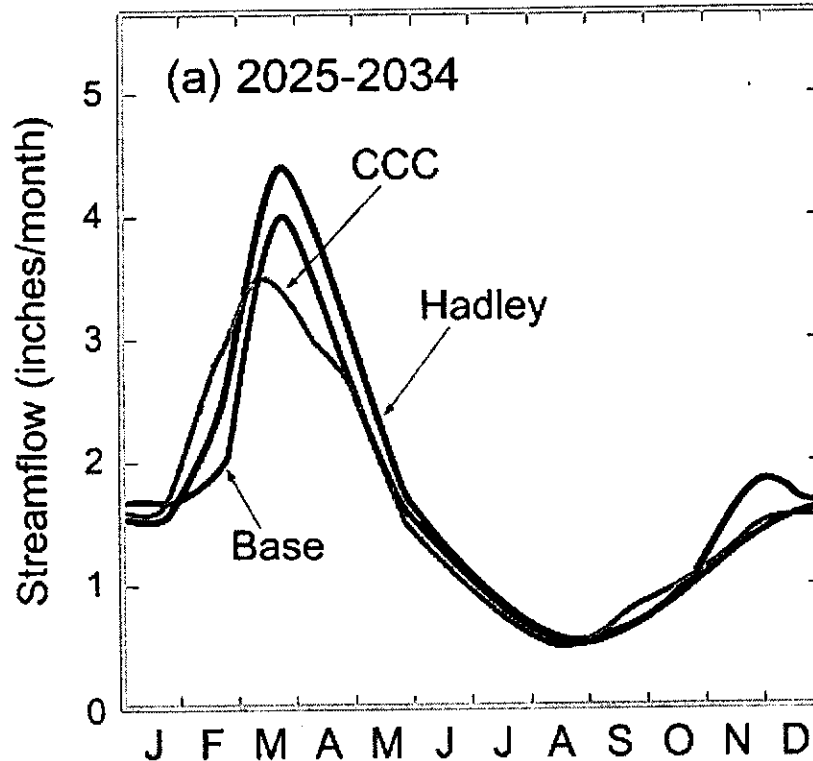


Figure 3. Simulated flow at the mouth of the Susquehanna River for the 1985–1994 base period and for the Hadley and CCC models for 2025–2034. Source: Fisher et al. 2000.

multaneously influenced by freshwater inflow, sea level, surface wind fields, and coastal landforms. Less mobile or coastal spawning subtropical shellfish and fish species might not quickly increase their use of the Bay for these reasons. In addition, northern range extensions (as a response to warming temperatures) of oligohaline–upper mesohaline species that live only in estuaries, such as the bivalves *Mytilopsis leucophaeata* or *Ischadium recurvum*, are likely to be inhibited or prevented (unless aided by human actions) by their inability to tolerate and successfully migrate through the marine environments that separate coastal estuaries.

Sea Level Rise

Because sea level rise acceleration rates will depend both on the pace of ocean warming and on the dynamic response(s) of land-based ice masses, sea level rise projections vary among models and according to the assumption that must be applied to future climate change scenarios, such as the trajectory of future radiatively active gas emissions. Thus, the sea level rise projected over the next century is greater based on the CCC model,

in which the atmosphere heats up more rapidly, than under the Hadley Center model. Both projections, however, fall within the envelope of model estimates presented in the latest intergovernmental panel on climate change assessment (Houghton et al. 2001), namely an 8–12 cm rise by 2030 and a 21–70 cm rise by the end of the century. Adding an average regional subsidence rate of 1.7 mm per year to the latest IPCC estimates yields a relative sea level increase in the Chesapeake Bay of 13–17 cm by 2030 and 38–87 cm rise by 2100, with central estimates of 15 cm and 55 cm, respectively. These are just slightly lower than the estimates of relative sea level rise by the Mid-Atlantic Regional Assessment (Fisher et al. 2000), which were based on the 1996 IPCC projections and marginally higher subsidence rates.

This rise in sea level will have several consequences for the Chesapeake Bay ecosystem. It will increase the average depth of the Bay and its tidal prism, allowing salinity to intrude farther up the Bay and its estuaries. This effect may be at least partially offset by increased sedimentation in the estuary and could also be ameliorated or exacerbated by simultaneous changes in freshwater inflow. Higher sea levels will also increase ero-

sion, resulting in the loss of islands and the retreat of shorelines. Together these changes will alter coastal geomorphology and sediment processes, thus contributing to the aforementioned sedimentation of the Bay (Wray et al. 1995).

Perhaps of greatest concern with regard to fisheries, however, are the consequences of sea level rise on tidal wetlands. These wetlands are able to develop and be sustained only if they are able to aggrade sufficient soil (mineral sediments and organic matter) to maintain their intertidal position (Stevenson et al. 1986; Reed 1999). Consequently, tidal marshes are deteriorating in areas of relatively high relative sea level rise (due in the recent past to subsidence) and limited sediment supply. Not only do these wetlands erode along their margins, but they also fragment from within as marsh plants succumb to the anoxia or sulfide toxicity that attend excessive tidal inundation. Such deterioration has been observed in the rapidly subsiding Mississippi deltaic plain of Louisiana (Reed 1995, 1999) and in the Blackwater marshes of Chesapeake Bay (Stevenson et al. 1986; Wray et al. 1995).

The effects of accelerated sea level rise on tidal wetlands within Chesapeake Bay are likely to be exacerbated by efforts to protect coastal lands from erosion and inundation. Both shoreline development and bulkheading strongly inhibit landward migration of marsh plants and submersed vegetation by altering shoreline relief and depth profile (Short and Neckles 1999), so construction of protective structures, such as levees and berms, would prevent wetlands from migrating inland as sea level rises. Therefore, future wetland losses will be most dramatic in the extensive, very low lying eastern margins of the Bay (Titus and Richman 2001) and are not likely to be counterbalanced by wetland gains.

Large areas of tidal marshes of the lower Chesapeake Bay, in addition to the Blackwater marshes mentioned above, are already showing signs of internal deterioration reflective of insufficient sediment supply (Stevenson, this volume). Except for those intertidal wetlands in the upper reaches of the Bay and its tributaries that receive relatively high sediment loads, the long-term future of Chesapeake Bay tidal marshes is bleak. Furthermore, submerged aquatic vegetation is unlikely to become established over the shallow water bottoms left as emergent vegetation is lost to rising water levels because colonization would be inhibited by high erosion rates, high turbidity, and exposed overconsolidated clay soils likely to exist in these areas (Stevenson, this volume).

Reductions in tidal marsh and submersed vegetation directly affect the Bay's fisheries because many fishes and crustaceans utilize these habitats as nursery

areas and foraging grounds (e.g., Boesch and Turner 1984; Fredette et al. 1990; Fitz and Weigert 1991; Kneib and Wagner 1994). Ecologically and economically important species that utilize these habitats include forage fishes such as mummichog *Fundulus heteroclitus*, eastern mosquitofish *Gambusia holbrooki*, and predatory nekton such as summer flounder, spotted seatrout *Cynoscion nebulosus*, striped bass, and blue crabs *Callinectes sapidus*. Because many of these species spend much of their life spans in the coastal Atlantic, significant loss or degradation of these habitats would also affect the larger-scale Northeast U.S. Continental Shelf Large Marine Ecosystem.

Streamflow

Although estimated changes in annual streamflow based on Hadley (streamflow increases) and CCC (decreases) models disagree in sign (Fisher et al. 2000), the greatest changes predicted by both models occur during the winter-spring seasonal transition period (February–April). Because flow into Chesapeake Bay normally peaks during the late winter–early spring (with the exception of short-term extreme events such as tropical storms) and because streamflow is the dominant delivery mechanism of allochthonous nutrients to the estuary (Boynton et al. 1995), the magnitude and distribution of primary production and salinity are strongly influenced by the annual spring freshet (Glibert et al. 1995; Malone et al. 1996). A persistent drift (positive or negative) in the long-term mean streamflow during these months, therefore, would have significant impacts on the ecosystem. The Chesapeake Bay typically experiences wide variations in freshwater inflow and salinity over decadal and longer time periods (Cronin et al. 2000). The key question is whether 21st century climate changes will result in a secular shift in the amount, seasonality, and shorter-term variance of inflow.

Primary Production: Phytoplankton production and species composition generally follow predictable seasonal patterns dictated primarily by annual riverflow, light, and temperature patterns (Malone et al. 1996; Marshall and Nesius 1996). During the relatively low-light, cold, and turbulent winter–early spring period, centric diatoms dominate the flora. In most years, high flows during this period deliver nutrients that, along with warming temperatures, promote stratification of the water column and production of a mid-spring bloom of chain-forming diatoms. Stratification is well established during the warm, stable summer months when phytoplankton production peaks and the phytoplankton community is dominated by a picoplankton assemblage that includes small flagellates, small diatoms, and cyanobacteria. However, because the summer commu-

nity is dominated by picoplankton, a large proportion of this production is confined to the microbial food web loop (Malone et al. 1991) and is generally unavailable for fishery biomass production.

Fisheries production in the Bay, as in most mid latitude temperate systems, is strongly tied to the wave-like progression of annual production that originates with the spring diatom bloom and passes through the system to higher trophic levels (e.g., Cushing 1975, 1990; Silvert 1993; Pope et al. 1994). The secondary zooplankton bloom, supported by the spring phytoplankton bloom, serves as food for young of the year of spring spawning fishes and forage fish species of all ages. These small fishes in turn provide forage for larger fishes, the majority of which reside in the Bay on a seasonal basis. If the spring freshet should wane, or occur during warmer temperatures, after the seasonal transition from a diatom- to a picoplankton-dominated assemblage, fishery production would likely be negatively affected.

An example of this occurred in 1989, when the freshet occurred after the spring-to-summer seasonal transition. Because the succession to a summertime phytoplankton community had already taken place when the freshet occurred, nutrients delivered by the delayed freshwater pulse promoted unusually strong production of picoplankton instead of a spring diatom bloom (Malone et al. 1991). Because many economically important Bay species (summer flounder, striped bass, Atlantic menhaden, etc.) depend on spring zooplankton during their early life history stages, a long-term shift in the timing of the spring freshet could negatively affect fisheries production in the estuary. This scenario would also have implications for fisheries operating outside the Bay because many of these species spend much of their lives in the coastal ocean.

While changes in the timing and magnitude of freshwater flow could reduce the spring phytoplankton bloom, alterations in schedule of the winter-summer seasonal warming could also adversely affect fishery production. This is because altered seasonal temperature regimes could advance or retard the timing of the spring production bloom relative to the reproduction period of late winter and spring spawning fishes. Such shifts would likely cause a mismatch (as described by Cushing 1975, 1990) between the nutritional requirements of larval fishes and the abundance peak of their zooplankton prey. This is important because it is in these early life history stages that mortality rates establish the annual recruitment in many fish populations (Houde 1987).

Warming water temperatures may also alter the activity and abundance of predators that feed on fish eggs and larvae. There is strong evidence to suggest that warming of the winter water temperatures may be re-

sponsible for the decline in the winter flounder *Pleuronectes americanus* population in Narragansett Bay, Rhode Island. Keller et al. (1999) and Keller and Klein-MacPhee (2000) have shown that winter flounder egg and larval mortality rates are higher in warmer rather than cooler water temperatures (3°C difference). These authors noted that in their mesocosm experiments, egg and larval predators were more active and more abundant in warmwater mesocosms, and hatching winter flounder larvae were larger under colder conditions. These results suggest that earlier seasonal warming would result in reduced recruitment of winter- and spring-spawning fishes as the degree of temporal overlap between their early life stages and predators of these stages is increased. While differential mortality favoring earlier spawning individuals in these populations could possibly compensate for this temperature-related increase in predation, it is difficult to estimate how many generations (years) this would take, or if these changes would simply result in a (northward with warming) shift in the affected species' distributions.

Salinity: In addition to influencing fishery year-class strength and biomass, streamflow could alter the distribution and abundance of important fishery species by altering the estuary's salinity regime. Modeling studies have estimated that Susquehanna River flow could change by -4% to +33% (Najjar 1999; Neff et al. 2000), resulting in a change of salinity at the head of the Bay between +3.5% to -27.5% (Gibson and Najjar 2000). Such changes would likely most affect immobile organisms such as bivalves and barnacles. However, because these and other Bay species are capable of coping with strong salinity variations often encountered within the estuary, distributional responses may be relatively benign.

The most pronounced effects of altered salinity distributions on fishery species may result from changes in the distribution and abundance of predators, prey, and pathogens. Because of the many complex species interactions within the Bay ecosystem, it is not possible to completely assess and describe the myriad potential responses of the system to altered salinity regimes. We list only a few examples in order to provide some insight into these potential consequences.

The eastern oyster *Crassostrea virginica* has traditionally been an important fishery species for the Bay. As recently as 1987, the Chesapeake Bay was the largest oyster producer on the Atlantic and Gulf of Mexico coasts (Haven 1987). While overfishing has historically played an important role in demise of this fishery, two oyster pathogens, *Perkinsus marinus* (Dermo) and *Haplosporidium nelsoni* (MSX), have contributed to the recent decline and prevented the population's recovery (Andrews 1996). Although the physiological salinity range of the oyster is 5-35 ‰, the range of its patho-

gens has confined the healthy population to salinities of less than about 15 ‰ (Haven 1987). Model and field surveys indicate that flow-related salinity fluctuations within the 10–20 ‰ salinity zones influence the range and infection rate of oysters by both pathogens (Burreson and Ragone Calvo 1996; Ford 1996; Cook et al. 1998; Paraso et al. 1999). Further, Paraso et al. (1999) found that freshwater discharges later than April had little or no effects on infection. Complicating projections of the response of these pathogens to climate changes is the fact that the prevalence of both species increases during warmer winters (Burreson and Ragone Calvo 1996; Ford 1996; Cook et al. 1998; Paraso et al. 1999; Ford et al. 1999).

Another example of complex species interactions that could result from changes in streamflow and influence the state of Chesapeake Bay fisheries involves the two dominant gelatinous zooplankton species (jellyfishes) within the Bay, the ctenophore *Mnemiopsis leidyi* and the medusa *Chrysaora quinquecirrha* (Purcell and Arai 2000). Both of these species feed directly on fish eggs and larvae (Monteleone and Duguay 1988; Govoni and Olney 1991; Cowan and Houde 1993), as well as on zooplankton prey species that also serve as important prey for adult forage fish and the early life stages of many other fish species (Cargo and Schultz 1966; Burrell and Van Engel 1976; Feigenbaum and Kelly 1984; Purcell 1992). Abundance of both jellyfish species appears to be suppressed by high flow (Cargo and King 1990; Purcell et al. 1999). However, temperature also plays a role and is positively related to production of *C. quinquecirrha* with high salinities (Purcell et al. 1999). Further complicating these relationships is the fact that *C. quinquecirrha* is an important predator of *M. leidyi* (e.g., Feigenbaum and Kelly 1984; Purcell and Cowan 1995).

Dissolved oxygen: Changes in freshwater inflow and temperature interact to change estuarine density stratification and circulation. Furthermore, both density stratification and temperature affect the availability of dissolved oxygen. In most years, Chesapeake Bay evolves from a cool well-mixed water column in winter to strongly stratified conditions during the summer. The spring freshet results in fresher, less dense surface water, overriding more saline, deep waters. The newly stratified water column facilitates the annual spring bloom of chain-forming diatoms because it allows them to remain suspended high in the water column where light and nutrients (delivered by the freshet) are plentiful. As summer approaches, warming surface waters and low wind conditions reinforce stratified conditions. As the supply of silica is exhausted in the water column the diatom bloom sinks to bottom waters (Conley and Malone 1992). As this organic matter is consumed and

decomposed (oxidized) by lower water column organisms, dissolved oxygen in waters below the density gradient is reduced and regenerated nutrients are released (Malone et al. 1986). This leads to low oxygen conditions (hypoxia or anoxia) throughout much of the estuary's deeper water habitat. These low oxygen conditions have greatly intensified since the 1960s, commensurate with increases in nutrient loading (Boesch et al. 2001).

Seasonal hypoxia results in mortality of benthic animals in the deeper parts of the Bay, such that benthic macrofauna are essentially absent in the summer and depauperate during other times of the year (Holland et al. 1987; Sagasti et al. 2001). Mortality of benthic animals can also occur in shallow-water environments with episodic advection of hypoxic or anoxic bottom water shoreward (Breitburg 1990).

Although hypoxic or anoxic mortality events may become more frequent with higher flow, low dissolved oxygen concentration may have stronger effects upon the ecosystem and its fisheries through behavioral and physiological responses by organisms that alter trophic interactions over broad time and space scales (Breitburg et al. 2001). These alterations may act directly upon economically important species. For example, increases in summer temperatures and increased anoxia or hypoxia may exclude species such as striped bass and Atlantic sturgeon *Acipenser oxyrinchus* from benthic feeding grounds and bioenergetically favorable cool deep-water environments (Coutant 1985; Price et al. 1985; Coutant and Benson 1990; Brandt and Kirsch 1993; Secor and Gunderson 1998). Low dissolved oxygen can also alter trophic interactions that support fishery species by inhibiting production of ecologically important zooplankton grazers (Roman et al. 1993), increasing some species' susceptibility to predation (Breitburg et al. 1994, 1997) and providing predatory refuge to others (Sagasti et al. 2001). Although the net results of such changes on ecosystem dynamics are difficult to predict, substantial increases in hypoxic and anoxic conditions would likely reduce overall system productivity.

Discussion

The Chesapeake Bay ecosystem is a robust ecosystem that continues to support valuable fisheries amid strong natural climate variability and despite anthropogenic activities that have perturbed the system for more than two centuries. Anthropogenic activities, such as land use changes and pollution, on Chesapeake Bay are most often associated with European colonization; however, Jackson et al. (2001) suggest that human activities, particularly fishing, significantly affected coastal ecosys-

tems such as the Chesapeake Bay for hundreds of years before this time. Although Native American societies undoubtedly had some effects on the Bay, as reflected in the many large archaic oyster shell middens throughout the region, agricultural practices and land development greatly increased nutrient input and sedimentation rate within the Bay from the Colonial era onward. Cooper and Brush (1993), for example, found that sedimentation rates have increased more than 10-fold over the last 200 years.

There is mounting evidence suggesting that the most rapid period of ecosystem change occurred over the last several decades as land use changes and eutrophication associated with growth of the human population within the Bay's watershed coincided with climatological fluctuations that resulted in increased flow (Brush and Hilgartner 2000; Cronin et al. 2000; Karlson et al. 2000). The coming decades will certainly feature continued increases in population and development in the region. Assuming that the effects of increasing atmospheric concentrations of radiatively active gasses begin to emerge in the coming decades, challenges facing fisheries management will increase substantially.

These challenges are not insurmountable. As proposed recently in a report on similar issues confronting the Gulf of Mexico coastal region (Twilley et al. 2001), the most effective strategy will involve mitigation of climate change effects upon the ecosystem, minimizing the potential watershed-level anthropogenic activities that could exacerbate climate changes, and human adaptation to changes that are inevitable. In order to effectively employ these strategies, a cooperative management structure involving regional fisheries managers, planners, politicians, the fishing industry, fisheries scientists, estuarine ecologists, and the general public will have to be constructed.

Fortunately, efforts to minimize and mitigate the impact of anthropogenic activities began in the Bay region more than twenty years ago (Boesch et al. 2001). A watershed-based multi-jurisdictional management structure was first proposed by the 1987 Chesapeake Bay Agreement and is currently serving to accomplish ecosystem restoration and management goals set forth in the most recent (2000) Chesapeake Bay Agreement. This management structure could be adopted and used as a template for confronting the challenges facing fisheries managers over the coming decades. Current efforts underway to construct a Chesapeake Bay Fisheries Management Plan and a trophically-based fisheries-ecosystem model may also prove useful when confronting climate change effects on the Bay and its fisheries.

Ultimately, facilitating scientists' and managers' abilities to understand, anticipate, and mitigate the effects of future climate changes on Chesapeake Bay will

depend upon the continuation of current monitoring and research programs focused upon understanding important processes and dynamics of the Chesapeake Bay ecosystem. In addition, new emphasis should be placed on research directed towards understanding how the Chesapeake Bay ecosystem has responded to historical climate variability. This historical analogy approach may be the most accurate method currently available for illustrating the types of changes that could occur to the Chesapeake Bay ecosystem and its fisheries as a result of future climate changes.

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